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AVIAN RESOURCE USE IN DOMINICAN SHADE COFFEE PLANTATIONS

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ABSTRACT.—We quantified foraging behavior of 19 bird species in shade coffee plantations in the Dominican Republic to document and evaluate their use of food resources in the shade overstory relative to the coffee understory. All species were observed foraging in the *Inga vera* overstory, and 18 of the 19 species had median foraging heights significantly above the median maximum coffee height. Eight species (42%) foraged exclusively in the canopy or subcanopy and not in the coffee understory. No species foraged exclusively in the coffee, although the Narrow-billed Tody (*Todus angustirostris*) foraged mostly in coffee. A negative correlation was found between a species' median foraging height in our shade plantations and its abundance in nearby sun coffee plantations. Invertebrates and nectar were the most important food items in the *Inga* overstory where 95% of the species gleaned leaf surfaces, 63% probed flowers, 58% gleaned or probed wood, 47% used epiphytes (for invertebrates or fruits), and 26% gleaned or probed *Inga* fruit. In contrast, birds in coffee foraged primarily for invertebrate prey as 42% of all species gleaned leaf surfaces, 21% gleaned or probed wood, 21% gleaned or probed fruit, and 5% probed flowers. The *Inga* overstory was an important foraging site for most species suggesting that plantations without a shade overstory (i.e., sun coffee) will have a lower diversity and abundance of food and hence are less attractive to birds than traditional shade plantations. *Received 5 May 1997, accepted 11 Nov. 1997.*

SINOPSIS.—Cuantificamos el comportamiento alimenticio de 19 especies de aves en plantaciones de café de sombra en la República Dominicana para documentar y evaluar el uso de estas del recurso alimenticio en el dosel en relación al sotobosque de cafetos. Todas las especies fueron observadas alimentándose en el dosel de *Inga vera*; y en 18 de las 19 especies la mediana de altura de forrajeo fue significativamente mayor a la mediana de la altura máxima del café. Ocho especies (42%) se alimentaban exclusivamente en el dosel y no en el sotobosque de café. Ninguna especie se alimentaba exclusivamente en los cafetales, aún cuando *Todus angustirostris* lo hacia primordialmente en el café. Una correlación negativa fue encontrada en la altura mediana de forrajeo y en su abundancia en nuestras plantaciones de café a la sombra y las plantaciones de café de sol cercanas. Los invertebrados y el néctar fueron las fuentes de comida más importantes en el dosel de *Inga* donde el 95% de las especies se alimentaban picoteando ("gleaning") la superficie de las hojas, el 63% probaba las flores, el 58% probaba o picoteaba la madera, el 47% usaba las epífitas (para colectar invertebrados o frutas) y el 26% probaba o picoteaba en las frutas de *Inga*. Por el contrario, las aves en el café primordialmente cazaban invertebrados, ya que el 42% picoteaban en las superficies de las hojas, el 21% picoteaban o proban las madera, el 21% picoteaban y probaban las frutas, y el 5% probaban las flores por su néctar. El dosel de *Inga* fue un importantísimo lugar de forrajeo para la mayoría de las especies, suguiriendo que las plantaciones que carezcan de un dosel con sombra (tal como el café de sol) tendrán una menor diversidad y abundancia de comida haciéndolas así menos atractivas para las aves que las plantaciones tradicionales de sombra.

Coffee plantations with a shade overstory can have an abundance of birds and provide habitat for some forest species (e.g., Wetmore 1916; Griscom 1932; Aguilar-Ortiz 1982; Beehler et al. 1987; Wunderle and Latta 1996; Greenberg et al. 1997a,b). Given the attractiveness of these agroforestry plantations for birds, Oldfield (1988) and Thiollay (1995) have suggested that such plantations could function as buffer zones for some tropical forest reserves by extending the area covered by overstory canopy. Unfortunately, the current trend in coffee cultivation is to eliminate the shade overstory as farmers convert to higher-yielding coffee grown in open sunlight (Perfecto et al. 1996). This "sun coffee" does not support forest species as often as is found in traditional shade coffee plantations (Borrero 1986, Wunderle and Latta 1996, Greenberg et al. 1997a), and requires higher inputs of fertilizers and pesticides (Greenberg 1994, Vannini 1994, Wille 1994, Rice and Ward 1996). The ecological implications of this change in coffee cultivation is especially important in northern Latin America and the Caribbean where coffee plantations cover approximately 2.7 million ha at mid-elevation sites which

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have already been extensively deforested (Rice and Ward 1996).

To encourage coffee farmers to retain their shade overstory, an effort is underway to promote the labeling of coffee packages designating a shade plantation origin (Greenberg 1994, Wille 1994, Rice et al. 1997). This labeling scheme would encourage environmentally conscientious consumers to purchase shade coffee, thereby using the marketplace to promote the maintenance of shade canopy trees in some tropical agricultural landscapes. However, before such a program is initiated, it is valuable to understand how wildlife use shade plantations and what attracts them to plantations.

Despite the potential value of shade coffee for bird populations, only Greenberg and coworkers (1997a) have quantified some aspects of resource use by birds in shade plantations. Therefore, the objective of this study is to describe where and how birds forage in shade coffee plantations to determine the food resources utilized by birds in shade coffee plantations in the Dominican Republic on the Caribbean island of Hispaniola. These observations will allow us to evaluate the importance of the shade overstory relative to the coffee understory in attracting birds to coffee plantations.

STUDY SITE AND METHODS

Fourteen shade coffee plantations (mean = 1.2 ha, range 0.1–8.7 ha) were sampled in the vicinity of Manabao (19° 6′ N, 70° 48′ W) and Jarabacoa (19° 9′ N, 70° 39′ W), La Vega province, at an altitude of 560–840 m in the Cordillera Central of the Dominican Republic. The plantations are located in a zone receiving an annual rainfall of approximately 1200 mm per year (Hartshorn et al. 1980) and classified as subtropical moist forest in the Holdridge life zone system (Anonymous 1967). One hundred meter transects run in the four major cardinal directions from each plantation (Wunderle and Latta, unpublished data) indicate that 75% of the land area surrounding the plantations is non-forest (67% pasture and 8% cultivation of low ground crops). Tree canopies cover 20% of the surrounding area (13% wooded arroyo; 5% coffee plantations; 2% pine) and the remaining 5% of the land area contains a miscellaneous mix of roads, buildings, rivers, etc.

We used 27 16-m diameter circular plots (0.02 ha) to quantify vegetation distribution in the plantations. A single plot was placed in the center of each small plantation (0.1–0.6 ha), and three to seven plots were placed at 100 m intervals in the larger plantations (2.5–8.7 ha). Within each plot we measured all stems at least 3 cm at 1.3 m from the base (DBH). Stems less than 3 cm were measured in belt transects of 1.7 m width along the four cardinal directions from the plot center. Each belt transect was sampled by walking the north, south, east, and west radii with outstretched arms and counting all vertical stems less than 3 cm contacted by the arms or chest at 1.3 m above the ground. Basal area of shrub and tree stems was calculated using the actual DBH measurements for stems at least 3 cm and an estimate of 1.5 cm DBH for each stem less than 3 cm.

Foliage heights were determined at 20 points located at 1.6 m intervals along the north, south, east, and west radii of each circular plot. A 3-m tall pole (2.0 cm diameter) marked at 0.5 m intervals was placed vertically at each sampling point. We recorded the presence or absence of coffee foliage touching the pole within each height class. For height intervals above 3 m, we sighted along the pole and recorded the presence/absence of foliage in each of the following height intervals: 3–4 and 4–6 m. We used the upper limit of each height category to calculate the median maximum coffee height based on the two highest categories in each plot.

Plantations were visited during three periods (24 October–16 November 1994, 9 January–1 February 1995, 13 March–5 April 1995). Foraging observations were made most often between sunrise and noon, but some observations were made in the late afternoon. Observations were made by walking slowly though a plantation until a foraging bird was located. A foraging event was recorded five seconds after an individual was detected to avoid a bias toward the more conspicuous feeding techniques such as aerial maneuvers. To characterize foraging maneuvers, only a single foraging event was recorded from an individual during a morning to avoid the problem of auto correlation inherent in sequence data (Wagner 1981). The height of the location of the first maneuver was measured with an optical range finder. We tried to observe as many different individuals as possible, but for the rarer species we estimate that a maximum of 20% of the total observations were derived from the same individual. For the very abundant Bananaquit (*Coereba flaveola*), it was necessary to limit a morning's observation to a maximum of 3 individuals. Ovenbirds (*Seiurus aurocapilus*) were common ground foragers in the plantations (Wunderle and Latta 1996), but difficult to observe and therefore it was not possible to include ground foragers in this study.

Foraging maneuvers were classified into three major categories. We use the term "glean" to designate all "near-perch" maneuvers in which the forager remains on a perch and picks a food item from the substrate surface. This category includes all forms of reaching, hanging, and lunging. The term "probe" is used to designate all "near-perch" maneuvers in which a forager remains on a perch and obtains a food item from the under surface by probing, gaping, or pecking. Finally, we use the term "hover" to include all aerial maneuvers in which the forager obtains a food item by leaving the substrate by leaping, or flying. While hovering, a forager can obtain food from a surface or the air by gleaning or from the under surface by probing.

The times between successive foraging maneuvers in the shade overstory and coffee understory were obtained by continuously dictating foraging observations into a cassette tape recorder. Each forager was followed for a maximum of 5 min or until it disappeared. Using a stop watch we calculated the average time between foraging maneuvers for each individual in which three or more successive foraging maneuvers were observed. The median time between each foraging maneuver was based on the means for each individual in the particular habitat (coffee or overstory).

Nonparametric statistical tests were used throughout the study because the data did not fit the assumptions of normality (Hollander and Wolfe 1973). Because of the absence of normality we used medians to describe central tendency and in the analyses, although we do provide means for descriptive purposes (foraging heights). Mann-Whitney U-tests were used to compare the median times between foraging maneuvers. A one-tailed Wilcoxon Rank Sum Test was used to test the null hypothesis that the median foraging height of a species was not above the median maximum coffee height. The variation in a species' median foraging height and its abundance in point counts or net captures (Wunderle and Latta 1996) was compared using a Spearman Rank Correlation. Multidimensional scaling (MDS) provided a quantitative method for defining foraging guilds useful for comparisons with other sites. Multidimensional scaling was used to visualize the foraging dissimilarities between 19 bird species in the plantations based on their proportional use of three different foraging substrates (*Inga vera*, coffee, other) and three food types (nectar, fruit/seed, animal). Dissimilarities were computed indirectly by use of Euclidean distances, which were standardized before MDS based on the Kruskal method with monotonic regression (SYSTAT 1992). All analyses were conducted using SYSTAT (ver. 5.3) on a Macintosh computer.

RESULTS

As expected, coffee had the greatest stem density in our plantations, although its contribution to the total basal area was relatively small because most stems were less than 3 cm DBH (Table 1). The predominant variety of coffee (*Coffea arabica)* in the shade plantations was the traditional "típica" variety, although "catorra" predominated in some of the larger plantations and was used to replace "típica" in some of the smaller plantations. The median maximum height of coffee in our plantations was 4.0 m, which defined the limit of the plantation understory. Bananas and plantains (*Musa* spp.) were also found in the understory, but constituted only a small proportion of the total basal area. Subcanopy trees included *Citrus* spp. and guava (*Psidium guajava*). *Inga vera* (Mimosoideae) predominated in the overstory and accounted for over half the total basal area of the plantations. The maximum canopy height averaged 15.6 ± 3.8 (SD) m and ranged from 9.2–22.0 m among the 27 plots. Other canopy trees such as rose-apple (*Syzygium jambos*), royal palm (*Roystonia* sp.), American muskwood (*Guarea guidonia*) and Caribbean pine (*Pinus caribaea*) were rare in the plantations, but were more common along the edges of some plantations.

TABLE 1. Species composition, basal area, and importance value of plants in shade coffee plantations near Manabao and Jarabacoa, Dominican Republic.

Species	Density of stems, <3 cm DBH (stems/ha)	Density of stems, ≥3 cm DBH (stems/ha)	Basal area of stems ≥3 cm (m^2/ha)	Importance value of stems ≥3 cm
Coffea arabica	6907	744	2.26	14.74
Inga vera	50	206	10.73	69.99
Musa spp.	0	133	1.45	9.50
Citrus spp.	58	52	0.15	0.98
Persea americana	0	9	0.37	2.40
Syzygium jambos	0	6	0.31	2.02
Roystonea sp.	0	2	0.04	0.26
Psidium guajava	0	2	0.01	0.07
Guarea guidonia	0	2	0.01	0.07

We observed a total of 24 species foraging in the plantations, but restricted our analysis to 19 species for which we had adequate sample sizes. Of the 19 species, 13 were permanent residents, five were winter residents (Nearctic migrants), and one was a spring–summer resident (Neotropical migrant).

Foraging rates.—Adequate foraging rate samples were obtained for only two species of Nearctic migrants. Median time between foraging maneuvers in Black-throated Blue Warblers (*Dendroica caerulescens)* did not differ significantly (Mann-Whitney U = 177, $P > 0.05$) between coffee (median = 6 sec., $n = 15$) and *Inga* (median = 6 sec., $n = 27$). However, the American Redstart (*Setophaga ruticilla)* had significantly (Mann-Whitney U = 253.5, $P < 0.001$) shorter intervals in *Inga* (median = 7 sec., $n = 25$) than in coffee (median = 11 sec., $n = 12$).

Foraging heights.—The shade overstory

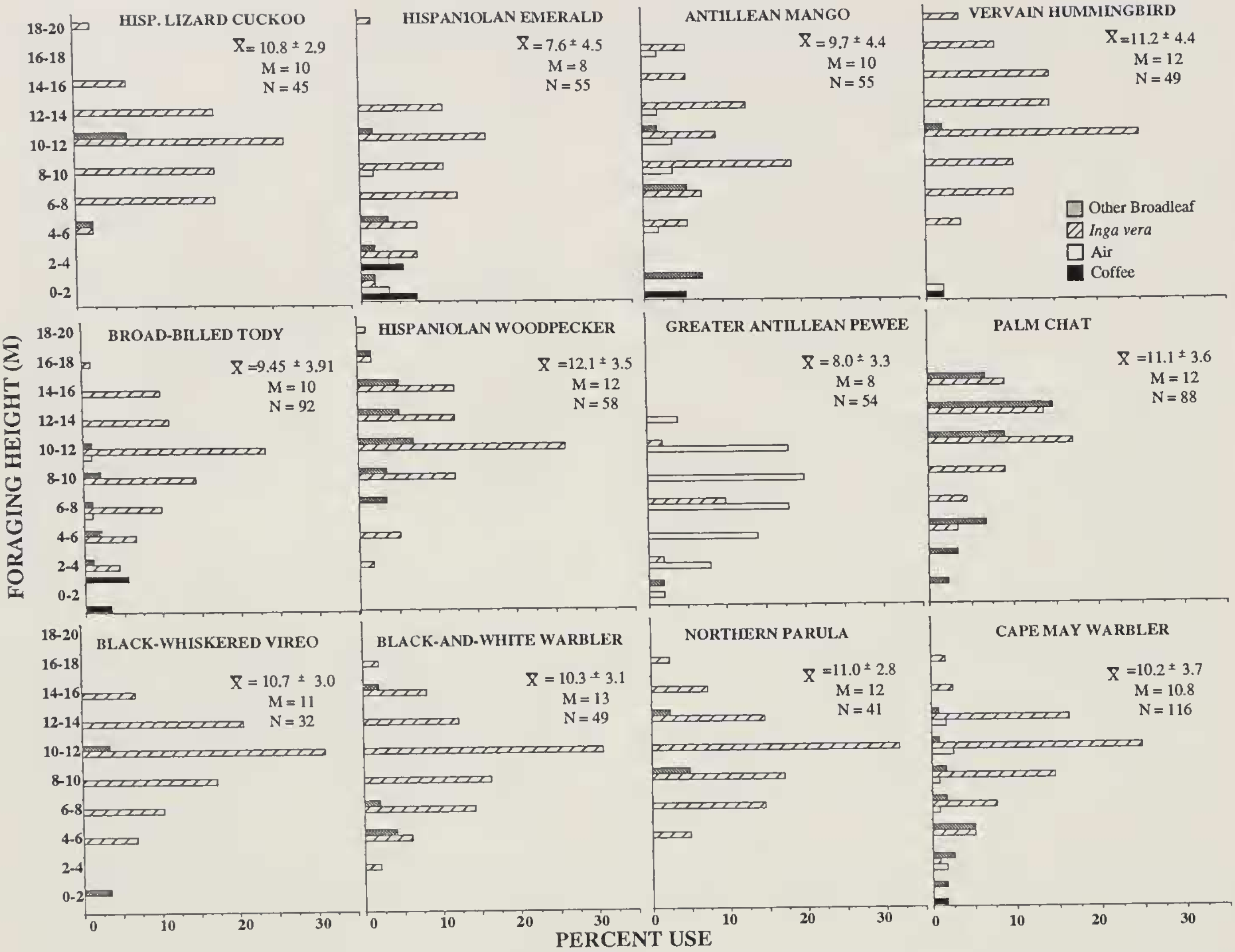

FIG. 1. Foraging height and location of first foraging maneuver after at least five seconds of observation for species in shade coffee plantations in the Dominican Republic. Foraging locations are given in legend. $\bar{X}$ refers to mean ± SD, M to median, and N to number of observations.

was the most important foraging site for almost all species, with 18 of the 19 species having median foraging heights significantly above the median maximum coffee height of 4.0 m (one-tailed Wilcoxon tests, all $P <$ 0.01). All species were observed foraging in the *Inga* overstory, although they differed in how they divided their time between *Inga* and the coffee understory (Fig. 1). Eight species (42% of 19 species) foraged exclusively in the canopy or subcanopy and were not observed in the coffee understory. These canopy dwellers included Hispaniolan Woodpecker (*Melenerpes striatus*), Hispaniolan Lizard Cuckoo (*Saurothera longirostris*), Palm Chat (*Dulus dominicus*), Black-cowled Oriole (*Icterus dominicensis*), Black-whiskered Vireo (*Vireo altiloquus*), Black-and-white Warbler (*Mniotilta varia*), Northern Parula (*Parula americana*), and Black-crowned Palm Tanager (*Phaenicophilus palmarum*). Only the Narrow-billed Tody (*Todus angustirostris*) foraged mostly in the coffee understory (67% of observations) as shown by its median foraging height which was below the median maximum coffee height (one-tailed Wilcoxon test: $Z = -3.61$, $P < 0.001$). Although it did not feed in the coffee, the Greater Antillean Pewee (*Contopus caribea*) sometimes perched on the coffee and fed in the airspace between the coffee and the *Inga* canopy.

Foraging height and presence in sun coffee.—We expected that species which foraged primarily in the shade overstory above the coffee would be less abundant in sun coffee plantations than species which foraged in the coffee below the shade overstory. We tested this expectation by comparing the median foraging heights of the 19 foragers with their abundance in point counts and mist net cap-

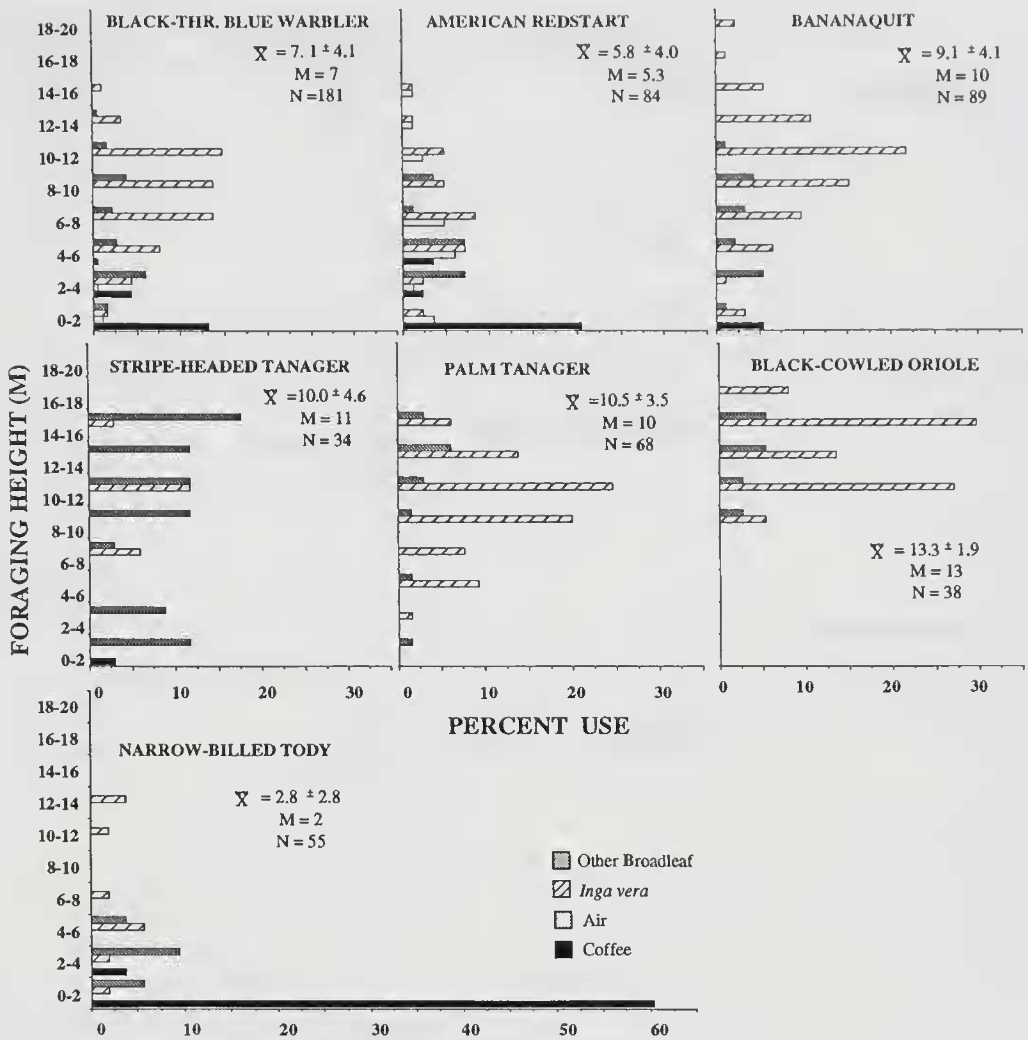

FIG. 1. Continued.

tures previously obtained in nearby sun coffee plantations (Wunderle and Latta 1996). As predicted, we found significant negative correlations between median avian foraging height in our shade plantations and abundance in sun coffee point counts (Spearman r = −0.62, df = 17, $P = 0.005$) and mist net samples (Spearman r = −0.58, df = 17, $P = 0.009$). Therefore, the higher a species forages in shade coffee plantations the less abundant it is likely to be in sun coffee plantations.

Foraging substrate.—Within *Inga* trees, the leaves were the most commonly used foraging substrate, on which 95% of all species (n = 19) foraged at least some of the time for invertebrate prey (Fig. 2). *Inga* leaves were the major foraging substrate (> 50% of observations) for Black-whiskered Vireo, Northern Parula, Broad-billed Tody (*Todus subulatus*), and Hispaniolan Lizard Cuckoo. *Inga* flowers were the next most important foraging substrate visited by 63% of the species. *Inga* flower visits accounted for over half the foraging observations for Vervain Hummingbird (*Mellisuga minima*), Black-cowled Oriole, Bananaquit, and Hispaniolan Emerald (*Chlorostilbon swainsonii*). The next most commonly used substrate was the *Inga* wood (trunk, branch, twig), upon which 58% of the birds foraged. *Inga* wood accounted for over half the observations of Hispaniolan Woodpecker (branches and trunk) and Black-and-white Warbler (branches and twigs). Less than half (47%) the species were observed feeding on or from *Inga* epiphytes. Epiphytes were gleaned or probed by 42% of all species but only 16% of all species consumed epiphyte fruits. Epiphyte foraging constituted only a small portion of a species' foraging visits, as evident in the two species which foraged most commonly on epiphytes: Stripe-headed Tanager (*Spindalis zena*; 36% of all observations, all fruit) and Black-crowned Palm Tanager (16% of all observations; 4 invertebrate, 6 fruit). *Inga* fruits were not present during most of the study. Perhaps as a result, they were the

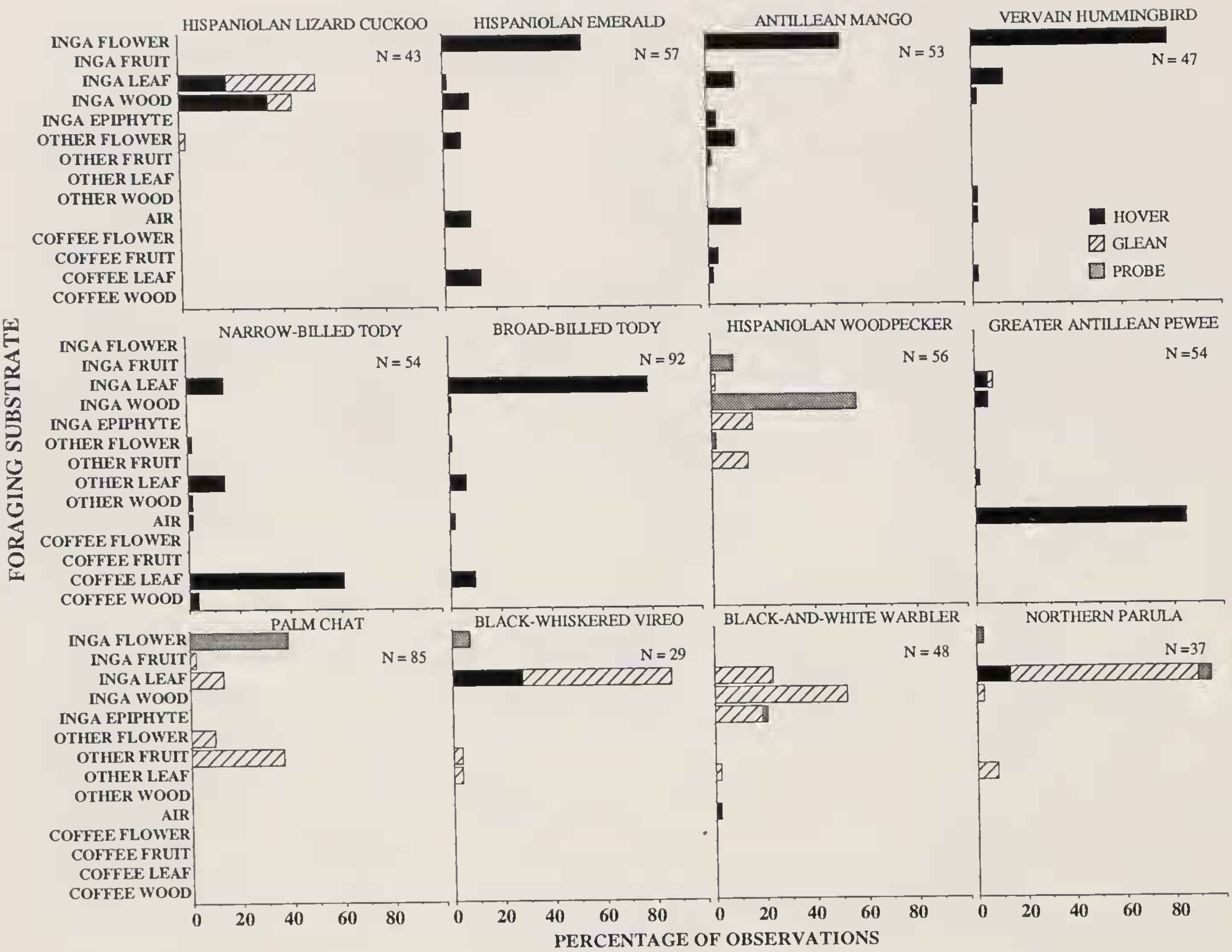

FIG. 2. Foraging substrates and three foraging maneuvers used by birds in shade coffee plantations in the Dominican Republic. Each observation (N) based on first substrate and maneuver used after at least five seconds of observation in a morning.

least commonly used substrate on the tree, used by only 26% of the species (mostly for invertebrate prey?), and at most, constituting only 9% of a species' foraging substrate (i.e., Hispaniolan Woodpecker).

Within coffee, the leaves were also the most commonly utilized substrate as evident in coffee leaf use by 42% of the 19 species. Coffee leaves were especially important for Narrow-billed Tody (62% of observations), but constituted less than a quarter of the foraging observations in the others (American Redstart, 24%; Black-throated Blue Warbler, 14%; Hispaniolan Emerald, 4%). The remaining parts of the coffee were used by only a relatively small percentage of the species (coffee wood, 21%; coffee fruit, 21%; coffee flower, 5%).

In addition to substrates in *Inga* and coffee, birds also foraged on substrates of the less abundant plant species. For example, flowers of other species (excluding coffee or *Inga*) were visited by 52% of the species, but at most constituted only about 10% of a species' diet (e.g., Antillean Mango, 11%; Bananaquit, 10%). *Syzygium* flowers were the most commonly used of the less abundant plant species (visited by 39% of the species). Fruits other than those of coffee and *Inga* were also consumed by 52% of the species, but constituted an appreciable portion of the diet in only two species (Palm Chat, 39%; Stripe-headed Tanager, 33%). The most important fruits appeared to be those of *Roystonea* (consumed by 28% of the species) and *Miconia* (consumed by 22% of species). In addition to leaves of coffee and *Inga*, 52% of the bird species fed from the leaves of a variety of other less abundant plants (8 plant species). At most these constituted only 12% of a species' foraging time (American Redstart). The most important leaves were those of *Citrus* spp. which were used by 21% of the species.

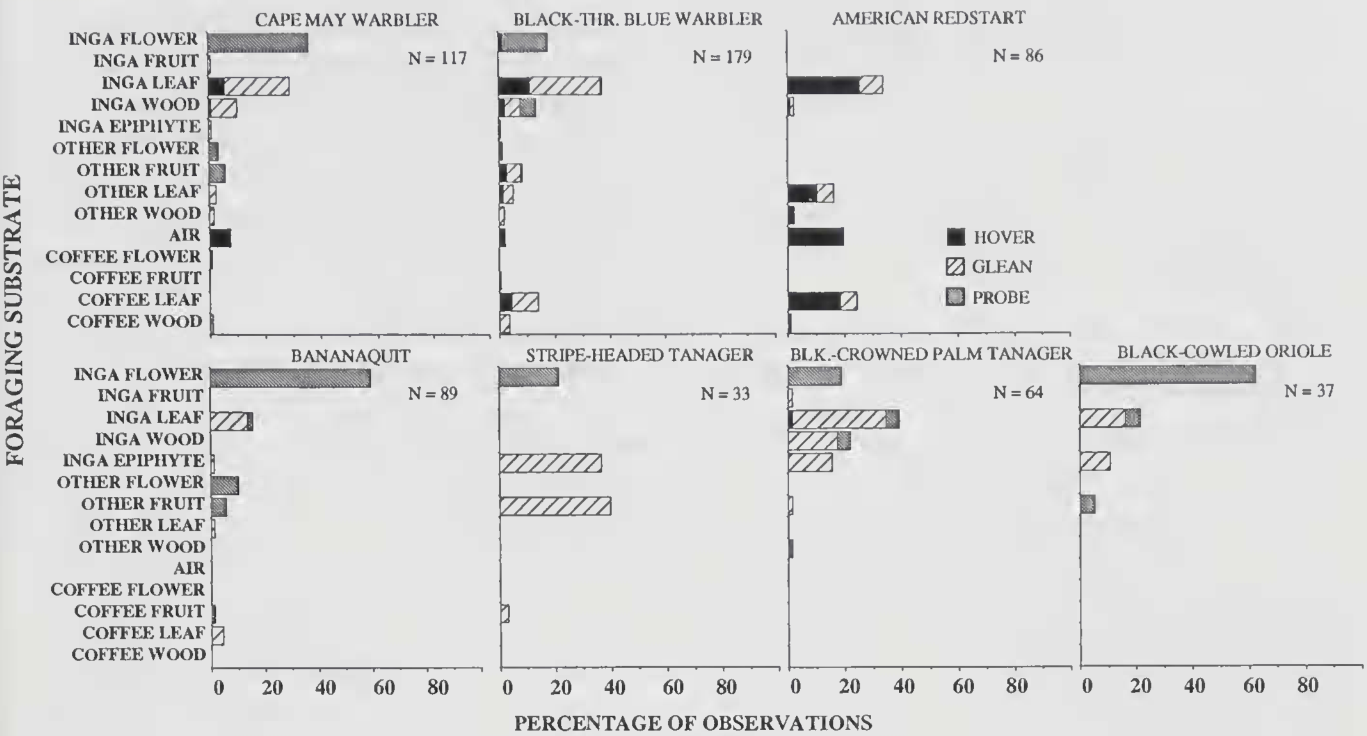

FIG. 2. Continued.

Foraging on woods other than coffee and *Inga* was uncommon and occurred in only 32% of the species and never constituted more than 2% of a species' foraging time.

Foraging maneuvers.—Individual species were usually consistent in their foraging maneuvers when feeding on similar substrates in coffee and *Inga* (Fig. 2). The only exception was the leaf probe maneuver used to obtain invertebrate prey from rolled or bound *Inga* leaves by Northern Parula, Black-throated Blue Warbler, Bananaquit, Black-crowned Palm Tanager, and Black-cowled Oriole. Leaf probing was absent in birds foraging in coffee, because there were no rolled or bound coffee leaves.

Species differed in their use of various foraging maneuvers while feeding in the plantations. For example, hovering was found in 68% of the species, but it was the predominant maneuver in only 42% of the species. Some species used hovering exclusively, such as hummingbirds which probed flowers or picked invertebrates from the air or leaf surfaces. Hovering also was the only maneuver used by both species of todies as they gleaned invertebrates from the undersides of leaves, and was the predominant maneuver used by Greater Antillean Pewees to capture insects in the air. Hovering was the predominant maneuver used by American Redstarts to capture invertebrates on leaf surfaces and in the air, although gleaning was also used. The leaps predominantly used by Hispaniolan Lizard Cuckoos to capture both lizards and invertebrate prey were classified as hovers, although cuckoos also gleaned prey from wood and leaf surfaces.

Gleaning was used by 68% of the species, although it was the predominant maneuver in only 32% of the species. Black-and-white Warblers gleaned mostly from wood surfaces or epiphytes on wood surfaces (lichens). Both Black-whiskered Vireo and Northern Parula commonly gleaned *Inga* leaves and, less frequently, hovered to take invertebrates from leaf surfaces. Gleaning prey from a variety of substrates with some probing characterized Black-crowned Palm Tanagers. Gleaning was the predominant maneuver used by Palm Chats, mostly to remove fruit, but they sometimes probed *Inga* flowers. Although gleaning was the predominant maneuver used by Black-throated Blue Warblers, they also hovered and probed a variety of substrates and were one of the most versatile foragers in the plantations (with Cape May Warbler, *Dendroica tigrinum*, see below).

Probing while perched on the substrate occurred in 53% of the species, but it was the predominant maneuver in only 26%. If the flower probes of hovering hummingbirds are

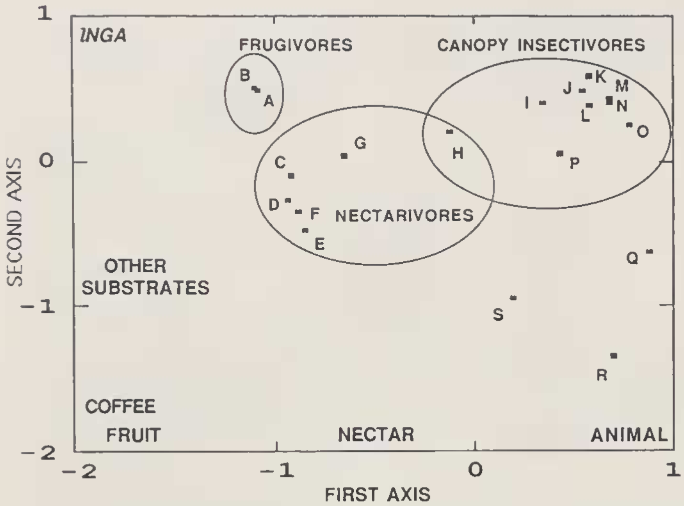

FIG. 3. Multidimensional scaling on two axis of foraging birds in shade coffee plantations in the Dominican Republic, based on three foraging substrates (coffee, other substrates, *Inga vera*), and three food types (fruit/seed, nectar, animal). Letters refer to the following species: A. Stripe-headed Tanager, B. Palm Chat, C. Bananaquit, D. Vervain Hummingbird, E. Hispaniolan Emerald, F. Antillean Mango, G. Black-cowled Oriole, H. Cape May Warbler, I. Black-crowned Palm Tanager, J. Black-whiskered Vireo, K. Hispaniolan Woodpecker, L. Northern Parula, M. Hispaniolan Lizard Cuckoo, N. Black-and-white Warbler, O. Broad-billed Tody, P. Black-throated Blue Warbler, Q. American Redstart, R. Narrow-billed Tody, S. Greater Antillean Pewee.

included, then probing occurred in 68% of the species, with 42% using it as the predominant maneuver. Probing was the predominant maneuver for Black-cowled Orioles, Bananaquits, and Cape May Warblers, primarily for nectar in flowers, but sometimes used for obtaining fruit juices. Hispaniolan Woodpeckers mostly probed wood, but also *Inga* fruit and flowers of *Syzygium*.

Foraging ordination.—Multidimensional scaling (MDS) enabled us to visualize dissimilarity among the 19 bird species based on their proportional use of foraging site and food type (Fig. 3). The first MDS axis separated species primarily on the basis of diet, with those species taking a high proportion of animal prey at one extreme on the axis in contrast to those with a high proportion of plant material on the other (nectarivory and frugivory). The second axis separated foragers on the basis of foraging site, with species foraging mostly in coffee at one extreme of the axis, in "other" plant category in the center, and in *Inga* at the other extreme. The third axis only weakly separated species foraging primarily in the "other" plant category from those foraging in *Inga* and coffee. Tight clusters were apparent for nectarivores, which fed mostly in the canopy (Antillean Mango, Hispaniolan Emerald, Vervain Hummingbird, Bananaquit, Black-cowled Oriole) and canopy insectivores (Black-crowned Palm Tanager, Hispaniolan Woodpecker, Hispaniolan Cuckoo, Broad-billed Tody, Black-whiskered Vireo, Black-throated Blue Warbler, Northern Parula, Black-and-white Warbler). Palm Chats and Stripe-headed Tanagers clustered together on the first two axes because of their tendency to feed on nectar from *Inga* flowers and consume fruit from other plants.

DISCUSSION

Given the preponderance of foraging observations in the *Inga* overstory, it is apparent that the characteristics of *Inga vera* strongly influence the foraging behavior and presence of birds in these plantations. Our finding that all species fed from *Inga* leaf surfaces at least some of the time, suggests that the *Inga* leaves in our plantations hosted an abundant invertebrate fauna. Indeed, *Inga* leaves are known to host a variety of invertebrates including folivores such as grasshoppers, katydids, lepidopteran larvae, and beetles and others that bind together leaves including spiders, small orthopterans, skipper larvae, and microlepidoptera (Koptur 1983). Although the extrafloral nectaries on *Inga* leaves may attract various ants, parasitic wasps, and flies that deter herbivores (Bentley 1977, Koptur 1983), no invertebrates were detected during our inspections of the nectaries on both young and old leaves. Caterpillars and leaf damage were often evident in the canopy and at times the frass rain was audible in some plantations. Not surprisingly, several bird species were observed feeding on caterpillars in the *Inga* canopy.

Flowers of *Inga vera* have nocturnal anthesis and are visited at night by bats and hawkmoths (Salas 1967, 1974), but evidently nectar remains in the morning when most bird visits were observed. *Inga vera* flowers have been found to be attractive to a variety of avian nectarivores during restricted flowering periods, at least in areas of seasonal rainfall (Wolf 1970, Greenberg et al. 1997b). In our plantations, some *Inga* flowers were present throughout the duration of our study, but flowers were most abundant in March–April (pers. obs.). Despite this seasonal variation in *Inga* flower abundance, the most abundant nectarivores visited flowers in the same proportions (relative to insectivory) throughout the study period, although the numbers of nectarivores increased with an increase in flowering (pers. obs.). The March–April flowering peak in this study was later than in the previous two seasons when flowering peaked in January. As a result of the later flowering, *Inga* fruiting was also delayed and most fruits had not ripened by the end of our study. Therefore it is likely that *Inga* fruit consumption was under-represented in this study relative to previous years when we occasionally encountered parrots and parakeets feeding on *Inga* pods during the same time period.

Epiphytes and plant parasites growing on the *Inga* were not abundant in our plantations, which undoubtedly explains their relatively low levels of use by most birds. Lichens were the most abundant epiphytes and were probed or gleaned for invertebrates by several species including Black-and-white Warbler, Hispaniolan Emerald, Black-throated Blue Warbler, and Hispaniolan Lizard Cuckoo. Bromeliads were probed for invertebrates by Black-crowned Palm Tanagers, Hispaniolan Woodpeckers, Bananaquits and Greater Antillean Grackles (*Quiscalus niger).* Mistletoe fruits were consumed most frequently by Stripe-headed Tanagers, but were also taken by Black-crowned Palm Tanagers and Black-cowled Orioles. Also, Antillean Euphonias (*Euphonia musica*) probably would have been more abundant in our plantations had mistletoe been more common given the reliance of euphonias on mistletoe fruit (Snow 1981).

Almost all of the foraging maneuvers in coffee were associated with insectivory (includes insects and spiders). This preponderance of insectivory is consistent with mist net results from the same plantations (Wunderle and Latta 1996). These results, based on diet classification from the literature, indicate that 50% of the 358 birds captured in the coffee were primarily insectivorous compared with 43% nectarivores and 6.7% fruit/seed eaters. Given our foraging observations, it is likely that most of the captured nectarivores were actually feeding on invertebrates in the coffee when captured. Thus, it appears that foraging birds use coffee plants primarily to obtain invertebrate prey.

Despite the preponderance of foraging for invertebrates in the coffee, most birds foraged infrequently in coffee, and for American Redstarts the foraging rates were lower in coffee than in the *Inga* overstory. These findings undoubtedly are due to relatively low invertebrate densities on the coffee plants as noted by Greenberg and coworkers (1997a) who found arthropod biomass per 100 g leaf biomass to be approximately 6 times greater for *Inga* than shade coffee. Evidence for low densities is also supported by our observations that insect damage to coffee leaves was rare in contrast to the obvious damage in the *Inga* canopy (pers. obs.). Indeed, others have noted that insect damage to coffee leaves is unusual (Le-Pelly 1973), in part because young coffee leaves have an abundance of protective alkaloids and the older leaves are very tough (Frischknecht et al. 1986). Also, it is likely that the transfer of coffee to the Neotropics left behind many of the Old World herbivores that evolved mechanisms to overcome its defenses, as often occurs with the transfer of cultivated plants (Perfecto et al. 1996). Our own surveys of invertebrate abundance on coffee leaves in these plantations (Wunderle and Latta 1996) indicate levels of abundance three times lower than are found in native, moist broadleaf forest elsewhere in the Caribbean (Askins and Ewert 1994).

Given the importance of the overstory to avian foragers in our plantations, it is not surprising that canopy dwellers were less abundant in the absence of a canopy in nearby sun coffee plantations (Wunderle and Latta 1996). For instance, of the 9 species that foraged exclusively in the *Inga* overstory, seven (Black-cowled Oriole, Black-whiskered Vireo, Greater Antillean Pewee, Hispaniolan Lizard Cuckoo, Palm Chat, Northern Parula, Black-and-white Warbler) were absent from point counts in sun coffee; Hispaniolan Woodpeckers were present in the sun coffee, but significantly less frequently; and Black-crowned Palm Tanagers were less frequent in sun coffee, but not significantly. Our observations indicate that nectarivores (Vervain Hummingbird, Hispaniolan Emerald, Antillean Mango, Bananaquit, Cape May Warbler) mostly fed on *Inga* flowers in the shade plantations, and as expected in the absence of flowering, each showed significantly lower abundance in sun coffee. Insectivores that fed mostly in the *Inga,* but descended into the coffee were also found in the sun coffee at counts equivalent to (American Redstart, Broad-billed Tody), or significantly higher (Black-throated Blue Warbler) than counts in shade plantations. Finally, the insectivorous Narrow-billed Tody foraged mostly in coffee and was also significantly more abundant in sun than shade plantations. Thus, species most dependent on the shade overstory for foraging are most likely to decrease in the absence of a shade overstory in sun plantations, while those that can forage in the coffee may be present, if not abundant, in some sun plantations (assuming low or no pesticide use).

Other cultivated crops in our plantations provided foraging opportunities, but they did not appear to be utilized disproportionately in relation to the plants' abundance. For example, bananas and plantains, despite their relative abundance in the plantations were infrequently used by foraging birds. The leaves were only rarely gleaned for invertebrates and the flowers sometimes visited for nectar (Antillean Mango, Bananaquit, Cape May Warbler). Other plants such as citrus, avocado, and guava appeared to be utilized by foragers in direct proportion to their abundance in the plantation. Although these crops may not have attracted additional bird species to the plantations, they may contribute to a plantation's attractiveness to birds by providing resources out of synchrony with the *Inga* overstory. In addition such sub-canopy trees as citrus and avocado provide additional foliage layers below the *Inga* canopy that serve as additional foraging substrate for insectivores.

Some of the non-agricultural plants in the plantations appeared to be important in attracting birds to the plantations. For example, royal palms attracted Palm Chats and Black-cowled Orioles. Both species were present only where palms occurred in the immediate vicinity, presumably because of nesting requirements, although Palm Chats frequently fed on palm fruit. Royal palm fruits are consumed by a diversity of species (Wunderle, unpubl. data), and the rarity of palms limited our fruit consumption observations to only 5 species. Fruits of the Melastomataceae are also known to be important for a variety of bird species (Snow 1981), but their rarity too may have limited our observations to only 4 species, all of which fed elsewhere in the plantations. *Syzygium* flowered throughout the duration of the study and was visited by 7 species, all of which were common at *Inga* flowers.

The results of our study suggest that a coffee plantation's attractiveness to birds is enhanced with the abundance, variety, and consistency of food resources in a plantation. This finding applies mostly to the shade overstory or plantation border, as the coffee plants alone provide limited food resources or foraging substrates for most species in this study. A diversity of plant species in the overstory or border attracts more birds, particularly if the plants are asynchronous in flowering and fruiting and extend the time period over which resources are available in a plantation. Given these traits, shade coffee plantations can provide food resources for a variety of bird species in agricultural areas, and thereby help maintain avian abundance and diversity in agricultural regions. Furthermore, these findings suggest that shade coffee plantations could serve as an effective buffer between forest reserves and surrounding agricultural landscapes.

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